

Estimating Survival and Recruitment in a Freshwater Mussel Population Using Mark-recapture Techniques

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ABSTRACT.—We used a mark-recapture method and model averaging to estimate apparent survival, recruitment and rate of population growth in a native freshwater mussel population at a site on the Cacapon River, which is a tributary to the Potomac River. Over 2200 *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa* were uniquely tagged over a period of 4 y. Recapture probabilities were higher in spring and summer than in winter except for *L. cariosa* which had a low probability of recapture regardless of time of year. All three species had high annual adult survival rates (>90%) with lower estimated survival of small (≤ 55 mm) mussels (43%–69%). The variation in apparent survival over time was similar for all three species. This suggests that whatever environmental variables affect survival of mussels in this site affected all three species the same. Recruitment rates were low (1–4%) for both *E. complanata* and *L. cariosa*, with *E. fisheriana* having several periods of high (15–23%) recruitment. Distribution within the site was affected by both downstream and upstream movement, though movement rates were generally <1%. Average population growth rates for *E. complanata* ($\lambda = 0.996$, SE = 0.053), *L. cariosa* ($\lambda = 0.993$, SE = 0.076) and *E. fisheriana* ($\lambda = 1.084$, SE = 0.276) indicated static populations. Population growth rate approximating 1.0 suggests this site supports a stable freshwater mussel population through a life history strategy of low but constant recruitment and high annual adult survival.

INTRODUCTION

Unionid mussels are one of the most imperiled fauna in the world (Williams *et al.*, 1993; Ricciardi and Rasmussen, 1999) with populations continuing to decline accompanied by a growing concern for the loss of species. The decline in many populations can be linked to development associated with expanding human populations which often leads to extensive habitat alteration and destruction that continue to impact North America's freshwater fauna. Attempts to address the cause of these declines is often limited by insufficient knowledge of the ecology of unionid populations. Consequently, monitoring freshwater mussel populations has begun to receive increasing emphasis. The objective of monitoring is often to detect differences in the life history traits between species within a population, or differences between populations over space and time, with the assumption that these differences may indicate a change in overall fitness as reflected in changes in recruitment and survival (Manly, 1985). The important dynamics in populations, such as recruitment and survival, are usually dependent on natural processes that vary across time. Therefore, monitoring of unionid populations is a long-term commitment to detect real changes in population parameters. While basic life history of unionid mussels has been studied since the early 1900s, rates of recruitment, survival and movement have not been well documented. Because these factors influence the rate of population change, our ability to evaluate population viability is limited.

Measuring survival rates in populations is often difficult and complex, with the probability of survival varying not only with individual characteristics, such as age, but with biotic and abiotic environmental variables as well. Estimating survival rates and testing hypotheses pertaining to survival are vital not only to understanding population dynamics but in developing effective management and conservation efforts. These population parameters

can often only be determined in the field from the study of uniquely marked individuals followed over time. Use of marked individuals and mark-recapture models are commonly used for population monitoring and risk assessment in many biological populations (Pollock *et al.*, 1990; Lebreton *et al.*, 1992; Anderson *et al.*, 1995; Schwarz and Seber, 1999), but have rarely been used to assess mussel populations (*see* Anthony *et al.*, 2001; Hart *et al.*, 2001; Rogers *et al.*, 2001). Mark-recapture studies typically involve repeated sampling of a target population allowing for recognition of uniquely marked individuals previously sampled. A variety of marking techniques exist for uniquely identifying animals (Seber, 1992) that allow us to analyze the specific capture history and movements of each individual animal. Each animal is marked when sampled for the first time, released back into their habitat and then has a chance of being recaptured on subsequent sampling occasions. On each sampling occasion the numbers of marked and unmarked animals are recorded. The marked animals are followed over time to estimate survival and capture probabilities (Cormack, 1964) and the ratio of marked to unmarked animals is used to estimate number of new recruits to the population (Burnham *et al.*, 1987). The unifying characteristic of multiple release mark-recapture data is there are known releases in separate independent cohorts. Animals in these cohorts are then subject to a survival process about which biologists wish to make inferences. The released cohorts are the samples and the resulting multiple counts of live animals provide the basis for inferences about the survival process.

Parameters in mark-recapture models (*e.g.*, recapture rate, survival rate) are estimated by finding the rate that minimizes the difference between the observed recapture values and the recaptures as predicted by the models. There are a number of assumptions for proper application of mark-recapture models. Some of the assumptions depend on the study design, such as the tagging, capture and recapture procedures. For example, it is important that tags are not lost or become illegible, recaptures must be recorded accurately, tagging and handling must not affect the survival or capture of animals and tagged animals must be representative of the target population. Other assumptions depend on the behavioral characteristics of the animals. For example, the fate of one tagged animal must not be linked to the fate of others. Violations of these assumptions can bias estimates to varying degrees (Carothers 1973, 1979; Pollock *et al.*, 1990). For example, because unionids are long-lived, it is important the marking method that is used is durable and is not susceptible to high tag loss which can negatively bias parameter estimates. Our objective was to describe the dynamics of a freshwater mussel population under natural conditions. We used mark-recapture models for populations open to recruitment, mortality and migration to determine apparent survival rates, recapture probabilities, recruitment, movement and rates of population change. We believed these methods would be useful not only in evaluating population dynamics, but in risk assessment, specifically where there is a need to evaluate the effects of a site specific disturbance on changes in mussel populations.

METHODS

Study site.—We chose a long-term monitoring site on the Cacapon River, a 5th order tributary in the upper Potomac River drainage in eastern West Virginia. The river is approximately 180 km in length and lies within the Ridge and Valley physiographic province. Approximately 79% of the basin is forested, but disturbance from agriculture and increasing development in the watershed is a primary concern. The study reach was located at Davis Ford (River Kilometer, RKM 94) and was 240 m long with an average width of 35 m. We marked the reach into 12 20 m long bands that extended bank to bank. The upper bands were mostly pool habitat with areas of run, the middle bands were a long riffle and the lower bands were primarily run habitat.

Bands were labeled A through L, with A being the uppermost band and L designating the downstream band at the bottom of the study area.

Field methods.—Prior to initiating the study we evaluated various types of tags and adhesives. Long-term tag retention, legibility and short drying times were the main factors in deciding which tags and adhesives we would use. The combination of shellfish tag (Hallprint Inc., Holden Hill, New South Wales, Australia) and cyanoacrylate (Krazy Glue, Borden, Inc., Columbus, OH) was found to provide a good long-term marking method (Lemarie *et al.*, 2000). Based on the tag evaluation study, animals were kept out of the water a minimum of 2 min after tagging to allow time for the glue to dry. Survey and tagging was initiated in July 1996 with seasonal sampling and tagging occurring in January, April, June and October 1997. Beginning in July 1998 we sampled and tagged mussels annually during the summer when most animals are likely to be available at the substrate surface. For each sampling occasion all untagged animals were tagged and tag numbers were recorded for previously tagged animals.

We conducted timed searches within each of the 12 bands by snorkeling to cover the entire area. We attempted to equalize sampling effort among bands by limiting the search time within bands to one person hour. All animals seen at the substrate surface were collected and a uniquely coded tag applied to both valves to minimize losing information due to tag loss. Double tagging can be used to estimate tag loss for adjusting model estimates (Seber, 1982:94). We recorded species, length in mm, left and right valve tag numbers, band number in which the animals were collected and time spent sampling. All animals were then returned to the bands where they were collected.

We used an enclosure study to evaluate potential tag induced mortality. A total of 60 animals (30 tagged and 30 untagged) was randomly assigned to four enclosures placed immediately downstream of the study site. The enclosures were checked several times during years one and two of the study. The number of live and dead animals, species and tag numbers were recorded.

Data analysis.—Analysis involved choosing a set of candidate models testing the fit of the models to the data and model averaging to estimate population parameters. We used the software program MARK (White and Burnham, 1999) which provides parameter estimates and associated standard errors for models developed from data on the encounter histories of marked animals. To estimate apparent survival and recapture probabilities, we used the Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965; Brownie, 1987; Pollock *et al.*, 1990) for open populations, selecting models on the basis of the parsimony criteria and biological significance (Lebreton *et al.*, 1992). Apparent survival (S) is defined as the probability of surviving between successive sampling occasions given that the animal has not permanently emigrated from the site. The recapture rate (p) is the probability of an animal being seen on a sampling occasion given that it is alive. Since we expected apparent survival to vary by species and over time, we included models with both a group (species) and time effect to evaluate the importance of these variables on survival (g and t , respectively). To evaluate survival rates for small vs. large animals we used the design matrix to construct models where apparent survival is estimated conditioned on size (length) of individual animals as a covariate.

The multi-strata model (based on Brownie *et al.*, 1993 and Hestbeck *et al.*, 1991) was used to estimate the rate of upstream and downstream movement of animals between bands. Evaluating movement of animals required combining the 20 m bands into 40 m wide bands due to several bands having insufficient recaptures. We did not expect adult freshwater mussels to have an unlimited ability to move great distances in an upstream direction; therefore, we constructed models where we fixed the distance animals could move in an upstream direction.

We used models developed by Pradel (1996) to estimate recruitment (f) and the finite rate of population change (λ), where λ is the population size at time $i + 1$ divided by the population size at the initial time i . Recruitment is the number of new animals (from both reproduction and immigration) of a minimum detectable size in the population at time t per animal in the population at time $t - 1$. Our data indicated the minimum detectable size at the substrate surface is 20 mm. We were interested in whether the population was increasing ($\lambda > 1$), stationary ($\lambda = 1$), or decreasing ($\lambda < 1$). The additional assumption that the size of the study site remains unchanged must be met for estimating rate of population change. Having unequal time intervals between sampling occasions (seasonal versus annual), we annualized the time intervals prior to running the models to make the rates of survival, movement, recruitment and population change for each of the intervals comparable.

To evaluate the fit of our set of models to the data we used a parametric bootstrap Goodness-of-Fit (GOF) test on the most general model, *i.e.*, the model with the most parameters. If the structure of the general model adequately fit the data, then subsequent models that are constraints of the general model can be derived. These bootstrap simulations also provide an estimate of the over-dispersion parameter (\hat{c}) calculated as the observed deviance divided by the average of the simulated deviances ($\hat{c} = 1$ if the model fits perfectly). The Akaike Information Criteria (AIC_c) for small sample sizes was used to rank the candidate models relative to each other (Burnham and Anderson, 1998:46) and the ΔAIC_c , or difference between the model AIC_c values, was used for calculating the AIC_c weights. The better the model fit relative to the number of model parameters, the smaller the AIC_c and the larger the value of the AIC_c weight (w_i). Burnham and Anderson (1998) provide a framework for using the ΔAIC_c values to rank models from best to worst. Models with ΔAIC_c between seven and 10 should be considered plausible with models having $\Delta AIC_c \leq 2$ given the greatest support. There often is not one best model for describing the variation in the data. Instead, several similar models may be essentially equal for describing the data, resulting in parameter estimates having an additional component of uncertainty, *i.e.*, uncertainty associated with sampling plus uncertainty due to model selection. Model averaging as presented in Burnham and Anderson (1998) was used to arrive at our estimates, where parameter estimates were weighted across a set of the best ranked models, allowing model selection uncertainty to be incorporated as a component of variance. Model averaging also reduces bias in the parameter estimates, especially when there are a number of models with similar AIC_c values.

RESULTS

The mussel assemblage consisted of seven species, including *Elliptio complanata* (Light-foot), *E. fisheriana* (Lea), *Strophitus undulatus* (Say), *Alasmidonta varicosa* (Lamarck), *A. undulata* (Say), *Lasmigona subviridis* (Conrad) and *Lampsilis cariosa*. *Elliptio complanata* was the dominant species. We identified all *Lampsilis* as *L. cariosa* though there is some question as to which species is found in the upper Potomac River basin. It is uncertain whether *L. cardium* (Rafinesque), a species introduced into the upper Potomac River, has supplanted *L. cariosa* (Say) or whether they have hybridized. Similarity in coloration and morphology has led to taxonomic questions that necessitate a more accurate means of identification.

Data were collected from July 1996 through June 2000 representing eight sampling occasions. Number of animals sufficient to model survival rates were collected for three of the seven species; *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa*. Of these three species a total of 2251 animals were tagged with the majority (85%) being *E. complanata*. We tagged 1909 *E. complanata*, of which 504 were seen again, with 158 of those being multiple

TABLE 1.—Data array of observed recaptures for three species, where i = time of release, j = time period of recapture, $R(i)$ = the number of individuals captured in time i and released with tags back into the population (referred to as a cohort), $m(i,j)$ = the number of tagged individuals captured for the first time during interval j from the cohort released at time i , $r(i)$ = the total number of the $R(i)$ individuals released that are captured again, $m(j)$ = the total number of marked individuals captured in the j th sample, and $z(j)$ = the total number of captures at intervals $j + 1, \dots, k$ from releases in cohorts, R_1, \dots, R_{j-1}

Time i	$R(i)$	Observed recaptures for <i>Elliptio complanta</i> $m(i,j)$							$r(i)$
		$j = 1/97$	4/97	6/97	10/97	7/98	7/99	6/00	
7/96	515	10	24	54	8	26	37	34	193
1/97	48		8	8	1	2	2	1	22
4/97	254			50	10	24	22	16	122
6/97	451				11	50	59	34	154
10/97	75					7	8	8	23
7/98	299						52	35	87
7/99	436							61	61
$m(j)$		10	32	112	30	109	180	189	
$z(j)$		183	173	183	307	221	128	0	
Time i	$R(i)$	Observed recaptures for <i>Elliptio fisheriana</i> $m(i,j)$							$r(i)$
		$j = 1/97$	4/97	6/97	10/97	7/98	7/99	6/00	
7/96	47	1	0	6	1	1	4	1	14
1/97	4		0	0	1	1	1	0	3
4/97	14			4	1	1	2	1	9
6/97	43				2	3	4	5	14
10/97	14					0	5	0	5
7/98	30						5	2	7
7/99	75							7	7
$m(j)$		1	0	10	5	6	21	16	
$z(j)$		13	16	15	24	23	9	0	
Time i	$R(i)$	Observed recaptures for <i>Lampsilis cariosa</i> $m(i,j)$							$r(i)$
		$j = 1/97$	4/97	6/97	10/97	7/98	7/99	6/00	
7/96	30	1	0	0	0	0	3	4	8
1/97	4		0	0	0	0	1	0	1
4/97	11			2	0	0	2	0	4
6/97	26				0	1	3	4	8
10/97	11					1	1	1	3
7/98	18						0	4	4
7/99	27							4	4
$m(j)$		1	0	2	0	2	10	17	
$z(j)$		7	8	10	18	19	13	0	

recaptures. A total of 206 *E. fisheriana* and 136 *L. cariosa* were tagged with 50 and 30 being recaptured, respectively. *Lampsilis cariosa* had the lowest number of multiple recaptures. The complete data array of observed recaptures is presented in Table 1. Using the data for *E. complanata* to demonstrate, 515 marked animals were released July 1996 with 10 marked animals recaptured for the first time in January 1997, 24 in April, 54 in June and 8 in October, 26 in July 1998, 37 in July 1999 and 34 in June 2000 for a total of 193 recaptured from that cohort. The 48 animals in R_2 (Time 1/97) represent animals released that were

TABLE 2.—Statistics for the candidate set of live-recapture models

Model ^a	ΔAIC_c	np	AIC Weight
$S(g + t) p(t)$	0.00	11	0.36867
$S(t) p(g + t)$	1.33	11	0.18941
$S(t) p(t)$	1.71	11	0.15703
$S(g^*t) p(t)$	3.02	13	0.08144
$S(g + t) p(g + t)$	3.81	13	0.05478
$S(g + t) p(g^*t)$	4.78	17	0.03387
$S(t) p(g^*t)$	4.90	17	0.03177
$S(\cdot) p(t)$	5.55	8	0.02294
$S(g^*t) p(g^*t)$	5.56	18	0.02284
$S(\cdot) p(g + t)$	6.96	9	0.01136
$S(g) p(t)$	7.21	9	0.01001
$S(\cdot) p(g^*t)$	8.35	14	0.00567
$S(g) p(g + t)$	8.98	10	0.00415
$S(g^*t) p(g + t)$	9.06	16	0.00397

^a $S()$ and $p()$ indicate survival and recapture parameters are functions of the factors in parentheses. The letters g and t represent species and time effects. If group or time effects are not specified (\cdot), then the parameters are assumed to be constant. When the parameters are a function of group and time simultaneously, these factors can then interact fully (g^*t) or the effects can be additive ($g + t$). np is the number of parameters estimated

a mix of 38 individuals initially tagged in January 1997, plus 10 previously tagged animals that were recaptured on this sampling occasion. The highest numbers of animals released and/or captured occurred during the summer sampling occasions, with greater incidences of recaptures coinciding with increasing number of sampling occasions. Although the lowest number of individuals captured and tagged was during the second (winter) sampling occasion, almost 50% of those animals were seen again.

Apparent survival estimates.—One thousand bootstrap simulations indicated no obvious lack of fit of the general model ($P > 0.10$) with only minor over-dispersion ($\hat{c} = 1.35$). A total of 25 live recapture models were fit to the data; of these, 14 had a $\Delta\text{AIC}_c < 10$ (Table 2) indicating several of the models were nearly equal in describing the data. We averaged model parameters across the 14 best fitting models and found that 72% of the weighting came from the top three models. Apparent survival varied over time (94% of the weight came from models with S varying with time) as did recapture probabilities. Survival varied less by species (24% of the weight came from models with species-specific S), though the top model did indicate species was important in evaluating differences in apparent survival rates. This species effect was evident in the apparent survival estimate for the interval between the first and second sampling occasion (July to January) (Table 3). *Elliptio fisheriana* had lower estimated survival (0.50, $\text{SE} = 0.22$) than *E. complanata* (0.58, $\text{SE} = 0.20$) and *L. cariosa* (0.62, $\text{SE} = 0.24$). Estimated annual adult survival over the 4 y ranged between 0.50 and 0.99. The highest standard errors of the apparent survival estimates were associated with the January sampling occasion, indicating a lack of precision in the survival estimate due to the low recapture probabilities. Apparent survival for all three species increased between the second and third sampling interval (81% survival for both *Elliptio* species and 77% for *L. cariosa*) then remained high and fairly constant (99%), with a slight decrease (86–89%) between the fifth and sixth sampling occasion. The overall pattern in apparent survival was the same for all three species with a constant and parallel difference in the apparent survival estimates among species.

TABLE 3.—Model-averaged estimates of apparent survival (*S*) and recapture probability (*p*). Apparent survival pertains to the interval between sampling occasions and recapture probability pertains to a single sampling occasion

Time	<i>E. complanata</i>			<i>E. fisheriana</i>			<i>Lampsilis cariosa</i>		
	<i>S</i>	SE	95% CI	<i>S</i>	SE	95% CI	<i>S</i>	SE	95% CI
7/96–1/97	0.58	0.204	(0.19, 0.97)	0.50	0.221	(0.07, 0.93)	0.62	0.236	(0.16, 1.08)
1/97–4/97	0.81	0.342	(0.14, 1.48)	0.81	0.394	(0.04, 1.58)	0.77	0.329	(0.13, 1.41)
4/97–7/97	0.99	0.037	(0.92, 1.06)	0.99	0.039	(0.91, 1.07)	0.99	0.018	(0.96, 1.03)
7/97–10/97	0.99	0.027	(0.94, 1.04)	0.99	0.039	(0.91, 1.07)	0.99	0.046	(0.90, 1.08)
10/97–7/98	0.86	0.099	(0.67, 1.05)	0.86	0.131	(0.60, 1.11)	0.89	0.115	(0.67, 1.12)
7/98–7/99	0.99	0.056	(0.88, 1.09)	0.99	0.018	(0.96, 1.02)	0.99	0.018	(0.96, 1.02)

Time	<i>E. complanata</i>			<i>E. fisheriana</i>			<i>Lampsilis cariosa</i>		
	<i>p</i>	SE	95% CI	<i>p</i>	SE	95% CI	<i>p</i>	SE	95% CI
1/97	0.03	0.021	(0.01, 0.07)	0.03	0.015	(0.00, 0.06)	0.02	0.026	(0.00, 0.07)
4/97	0.07	0.016	(0.04, 0.10)	0.06	0.027	(0.01, 0.11)	0.03	0.020	(0.00, 0.07)
7/97	0.18	0.020	(0.14, 0.22)	0.19	0.036	(0.12, 0.26)	0.08	0.041	(0.00, 0.16)
10/97	0.03	0.007	(0.02, 0.04)	0.04	0.015	(0.01, 0.07)	0.01	0.001	(0.008, 0.012)
7/98	0.12	0.016	(0.09, 0.15)	0.11	0.025	(0.07, 0.16)	0.05	0.026	(0.01, 0.10)
7/99	0.17	0.020	(0.13, 0.21)	0.18	0.030	(0.12, 0.24)	0.10	0.039	(0.02, 0.18)

The enclosure data indicated the lower survival rate between the first and second sampling occasion was not due to higher mortality from tagging nor did tagging affect mortality. Mortality in tagged and untagged individuals was the same (2%) after 1 y. Mortality increased to 12% after 2 y, with 4% mortality in tagged animals vs. 8% in untagged animals.

Recapture probabilities varied with time and species. Recapture probabilities showed seasonal variability with highest recapture rates (7–19%) occurring during the warmer periods of spring and summer and averaging about 3% in the fall and winter. *Lampsilis cariosa* had the lowest estimated recapture rates regardless of time of year.

We looked at annual and monthly stream flow from 1996 through 2000. The mean annual stream flow for the year 1996 was approximately 10% above the 74 year mean stream flow of 581 ft³/s, 1997 was below the long-term annual mean, 1998 was a high water year and stream flow for 1999 and 2000 was below normal (Table 4), with mean annual flow for 1999 approximately half of the long-term mean. Of note were the extreme high flows during the fall and winter of 1996 and the first half of 1998, corresponding with the low survival and recapture estimates over the fall-winter 1996 and the lower survival estimate over late winter to spring 1998. These high flows could have influenced the recapture rate estimate in the summer 1998 sampling occasion, which was lower than the summer 1997 and 1999 recapture estimates.

Apparent survival with size as a covariate.—We averaged model parameters over the five best models to estimate apparent survival based on size of individual animals. Small animals of all three species had lower estimated apparent survival with survival rate increasing with size (Fig. 1). A species effect was evident (67% of the weight came from models with *S* having a species effect), with *Elliptio fisheriana* having the lowest estimated rate of survival for small individuals, 43% for animals 20 mm in size versus 69% for *E. complanata* and 57% for *Lampsilis cariosa* of the same size. Difference in apparent survival among species was evident for animals between 20 and 55 mm in length with survival estimates becoming more similar with increasing size. *Elliptio complanata* ≥ 55 mm and *E. fisheriana* ≥ 75 mm in length had apparent survival rates >90%. *Lampsilis cariosa* ≥ 65 mm had apparent survival rate ≥90%.

TABLE 4.—Monthly streamflow statistics for the Cacapon River. The gage is located at Great Cacapon downstream of Davis Ford near the mouth to the Potomac River. The 74 year annual mean streamflow is 581 ft³/s, and the mean of monthly flows is based on data collected from 1923 through 2000

Year	Mean monthly streamflow in ft ³ /s												Mean annual stream flow
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	
1996	1166	381	497	358	725	386	351	198	61.7	851	1252	1486	643
1997	478	709	1452	462	307	521	118	94.5	91.1	99.2	1026	272	469
1998	1751	3234	2113	1406	1261	516	162	117	73.9		88.3	90.5	983
1999	300	169	791	550	209	72.5	53.8	56.7	198	343	179	430	279
2000	157	661	852	633	304	242	105	444	281				409
Mean	643	894	1286	1110	855	427	192	232	176	333	369	516	

Pradel's models.—We fit 59 candidate models for estimating recruitment rate (f); of these, 13 had a $\Delta\text{AIC}_c < 10$. We model averaged to arrive at our parameter estimate and found that 82% of the weighting came from the top four models. The most likely models for estimating the rate of recruitment indicated a strong species effect (98% of the weight came from models with f varying with species). Recruitment also varied over time (85% of the weight came from models with f having a time effect) with the top two models indicating an additive effect of group and time [71% weight for the $f(g + t)$ model parameter] for evaluating differences in recruitment rates. The species effect reflects the recruitment estimates for *Elliptio fisheriana* (Fig. 2), which had higher estimates and higher variability in the estimates. All three species showed the same general pattern of recruitment (*i.e.*, higher recruitment estimates for the same times of year). However, recruitment rate varied little over time for both *Elliptio complanata*, the dominant species in this assemblage, and *Lampsilis cariosa*, which is far less common. Highest estimated recruitment occurred for the first sampling occasion (summer-winter 1996) for *E. complanata* ($f = 0.037$, $\text{SE} = 0.058$) and *L. cariosa* ($f = 0.041$, $\text{SE} = 0.091$), with the remaining estimates slightly lower and constant. Highest estimated recruitment for *E. fisheriana* occurred over summer-winter 1996 ($f = 0.155$, $\text{SE} = 0.043$) and the summer 1998 to summer 1999 time period ($f = 0.225$, $\text{SE} = 0.25$). Lowest estimates were seen for the period of spring-early summer 1997 and again for the year July 1999 to June 2000 ($f = 0.001$, $\text{SE} = 0.005$), the same intervals of low to no recruitment for *E. complanata* and *L. cariosa*. While all three species had a higher annual recruitment rate for July 1998 through early summer of 1999, a decline in annual recruitment was seen for all three species for the following year.

Population growth rate (λ) increased after the first sampling occasion for all three species with a leveling off at a fairly constant rate for the remaining intervals (Fig. 3). Population growth rate was slightly negative for *Elliptio complanata* ($\lambda = 0.98$, $\text{SE} = 0.03$) and *Lampsilis cariosa* ($\lambda = 0.97$, $\text{SE} = 0.02$) for the interval of October 1997 to July 1998, with a slightly positive growth rate for *E. fisheriana* ($\lambda = 1.03$, $\text{SE} = 0.09$) for the same time period. *Elliptio fisheriana* had a static rate of population growth ($\lambda = 1.00$, $\text{SE} = 0.002$) between April and July 1997, with a positive growth rate estimated for winter-spring ($\lambda = 1.08$, $\text{SE} = 0.32$), summer-fall ($\lambda = 1.09$, $\text{SE} = 0.14$), fall-summer ($\lambda = 1.03$, $\text{SE} = 0.09$) with highest positive growth rate for the summer 1998 to summer 1999 period ($\lambda = 1.22$, $\text{SE} = 0.19$). There was little change in population growth (average $\lambda \approx 1$) from January 1997 through July 1999 for *E. complanata* and *L. cariosa*, with positive population growth (average $\lambda = 1.1$) for *E. fisheriana*. However, if the first interval is included then population growth rate over the four years was negative for

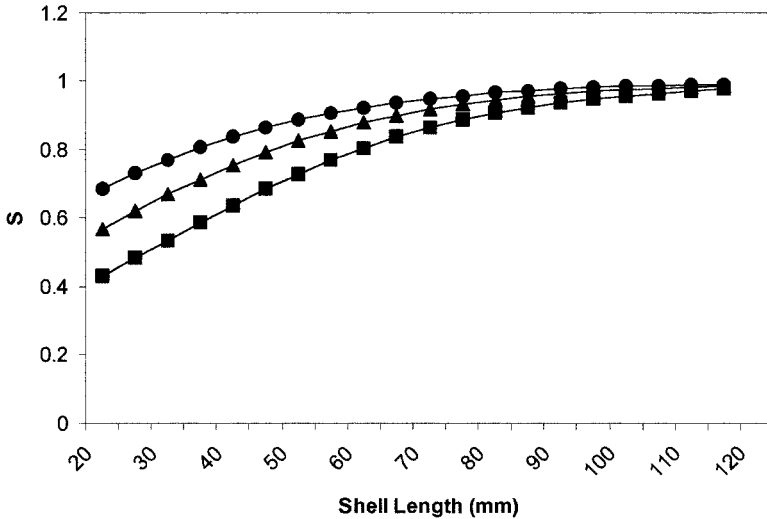


FIG. 1.—Apparent survival (S) modeled with length as a covariate for *Elliptio complanata* (circles), *E. fisheriana* (squares) and *Lampsilis cariosa* (triangles)

E. complanata and *L. cariosa* (average $\lambda = 0.96$) with slight positive population growth for *E. fisheriana* (average $\lambda = 1.02$) over the same four year period. Because the low recapture probabilities from the winter sampling occasion led to estimates of survival with large variances, we did not use the λ estimates (average 0.76, SE = 0.33) for the first interval.

Movement.—The estimated probability of moving between bands (ψ) was model averaged over four competing models. There was both downstream and upstream movement of animals within the site. Overall downstream movement for all species was less than 1% (average $\psi = 0.008$, SE = 0.003) (Fig. 4a). Most of the movement occurred within a distance of 40 m or less ($\psi = 0.009$, SE = 0.014) with some movement detected between 40 and 80 m in the downstream direction ($\psi = 0.007$, SE = 0.052). The majority of movement in the 0 to 40 m distance occurred from band A to band B ($\psi = 0.016$, SE = 0.031) in pool habitat at the top of the site (Fig. 4b) with lower but nearly equal estimates of movement throughout the remaining bands (average $\psi = 0.007$, SE = 0.014). Though we detected little movement in the 40 to 80 m distance, it did occur in all bands and was consistent among bands (Fig. 4c). Upstream movement occurred throughout the study site ($\psi = 0.04$, SE = 0.031) (Fig. 4a) with the majority of upstream movement occurring at the top of the site from band B to band A ($\psi = 0.13$, SE = 0.001) (Fig. 4d). The substrate in bands A and B where the animals were found was predominantly sand and silt, with mainly gravel and cobble substrates and higher flows in the remaining bands downstream. Eighty-nine percent of the weight came from the top model which fixed movement downstream at a constant rate but allowed movement to and from bands A and B to occur at a different rate (Table 5). The model structure reflected the habitat differences of bands A and B compared to the remainder of the site. The model that fixed all movement at a constant rate regardless of band had no support for describing the data.

DISCUSSION

Long-term studies of marked animals are essential to answering many of the questions fundamental to our understanding the population dynamics of freshwater mussels. Effective

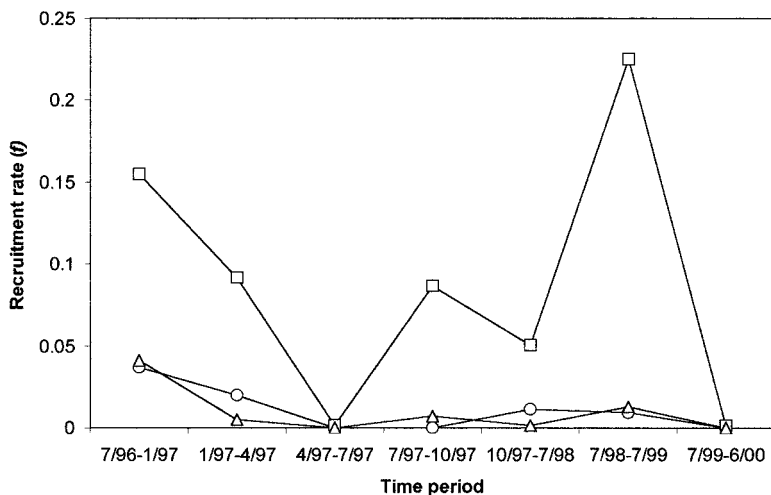


FIG. 2.—Recruitment rate estimates for *Elliptio complanata* (circles), *E. fisheriana* (squares) and *Lampsilis cariosa* (triangles). Recruitment rate (f) is the number of new animals of a minimum detectable size in the population at time t per animal in the population at time $t - 1$

management decisions rely on knowing something about the vital rates (survival, recruitment and movement) governing the population of interest. Survival is often difficult to estimate precisely because survival must be distinguished from the probability of seeing the animal again (Nichols, 1992). Mark-recapture studies require at a minimum 3 y to estimate the probability of recapture with a longer time frame required to arrive at more precise estimates if the recapture probabilities are low. The advantage of mark-recapture modeling is that it allows us to make separate inferences about survival and capture rates (Lebreton *et al.*, 1992) resulting in accurate estimates of survival on large samples of marked animals.

One of the study objectives was to estimate the survival rates of the species in the mussel assemblage at our study site. We developed the model structure on how we expect the parameter to vary; *e.g.*, is the probability of survival time, size and/or species-specific or is it constant over time? The various combinations of these variables led to a number of models identified as nearly equally useful for making inferences about the population. Though the top model was almost twice as well supported as the next best model, this was not sufficient evidence to be designated as the best model. We had three models that were feasible as a best model and a total of five models with sufficient evidence to also be considered as a possible best model. With this amount of model selection uncertainty it made sense to model average to arrive at our estimates. Since we followed one population and did not tag at multiple sites, we did exploratory analysis and did not focus on hypothesis testing. Our goal was to arrive at the best estimates of the population parameters based on our candidate set of models and not on finding the best model.

We expected the apparent survival rate for *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa* would vary over time, but we did not expect a nearly identical pattern of survival rates. *Elliptio complanata* is the overwhelmingly dominant species not only in this site but throughout the river and is considered to be a habitat generalist (Clarke, 1981), so we expected higher survival rate estimates than the two rarer species *E. fisheriana* and *L. cariosa*. *Elliptio fisheriana* was found only in areas of slow current and small particle size near the

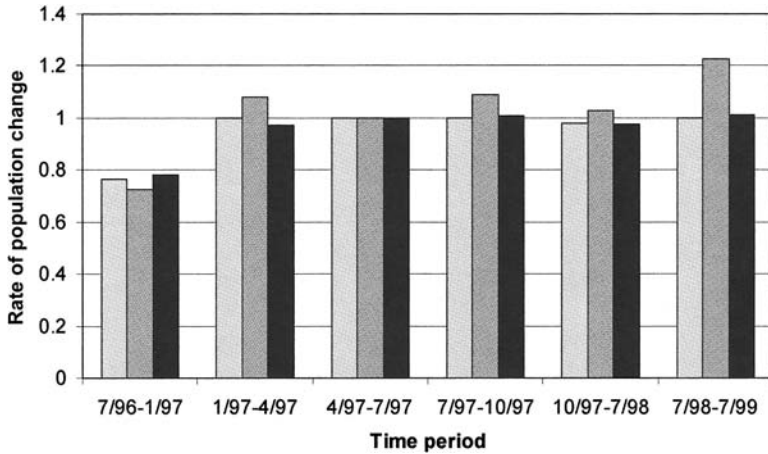


FIG. 3.—Rate of population growth (λ) for *Elliptio complanata* (light gray bar), *Elliptio fisheriana* (dark gray), and *Lampsilis cariosa* (black)

stream bank. These areas are often prone to drying during periods of drought, a common occurrence in this river, but the fine substrate may allow these animals to compensate by moving more readily to areas nearby that are still watered. It is also feasible these areas provide some protection during periods of high flow and scour events, enhancing survival rates and allowing animals to avoid being displaced (Downing *et al.*, 2000). *Lampsilis cariosa* is also found in low numbers but with a spatial distribution within the site similar to *E. complanata*. Though found in all substrate types and flows, *L. cariosa* was most often found almost completely buried within the substrate, possibly enhancing its survival.

Based on Akaike weights, time was the important predictor of apparent survival (94%) with very little species effect (24%) though the change in survival over time was small. Apparent survival approximated 1.0 (100%) for the intervals of late spring and summer and the last interval which represents an annual survival rate from July 1998 to July 1999 (Table 3). The winter through spring intervals had lower survival estimates with lowest estimated survival rate for the first sampling interval (fall to early winter). This presumed mortality was not induced by tagging, similar to results reported in other tagging studies (Kesler and Downing, 1997), nor was the estimate negatively biased due to tag loss since tag loss rate after 2 y was minimal (Lemarie *et al.*, 2000). We expected temporal variation in the recapture probabilities and our model estimates reflect this variation. Since the apparent survival estimate is dependent on the probability of being seen (captured) at a subsequent sampling occasion (Burnham *et al.*, 1987), the lack of precision of the survival estimates associated with winter sampling reflects both the low recapture probability (2–3%) in the January sampling occasion and, being early in the study, few capture occasions.

Factors influencing whether animals are at or below the substrate surface include temperature and day length, high flows and reproductive condition (Balfour and Smock, 1995; Amyot and Downing, 1991, 1997). *Elliptio complanata* begin moving to the surface in spring (often by late April at our latitude) with most animals at the surface in summer (June–July), they reburrow in fall and often remain there until the following spring (Amyot and Downing, 1998; Watters and O'Dee, 2001). For species that are short-term breeders, spawning in spring and releasing glochidia by fall, as well as some that are considered

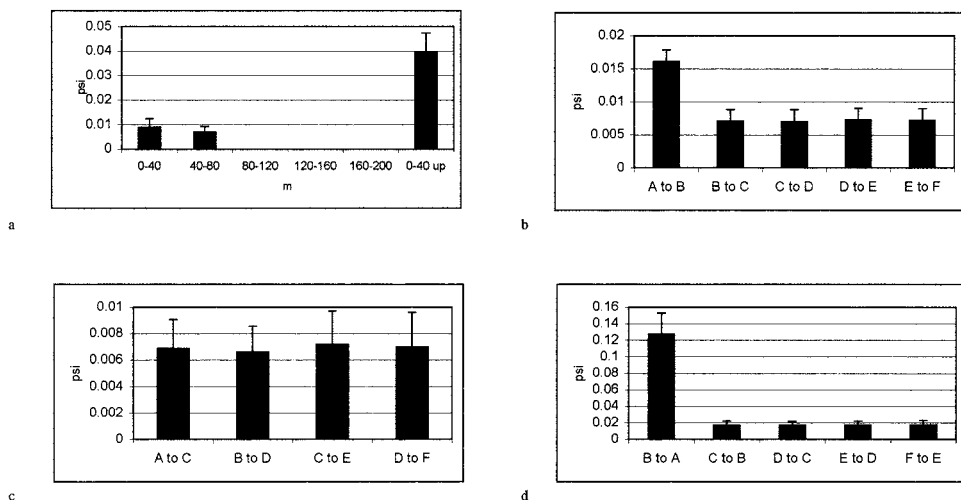


FIG. 4.—Estimates of rate of movement of *Elliptio complanata*, *E. fisheriana* and *Lampsilis cariosa*: a) distance moved in meters downstream and upstream within the site, b) within band downstream movement of 0–40 meters and c) 40–80 meters, and d) within band upstream movement, plus 1 SE. Letters A through F represent 40 meter wide bands with A being the band at the top of the site. ψ_i represents the probability that an animal moves from one strata (band) to another during interval i . Estimates of ψ_i are model averaged over 4 models

long-term breeders such as *Lampsilis cariosa*, this pattern of vertical movement to the surface is associated with spawning (Watters and O'Dee, 2001). Though we have found glochidia collected in drift samples in almost every month (R. Villella, pers. obs.), the peak periods of release were found from June to September. The two periods of low recapture were in January and October when temperatures (especially January 1997) were cold, flows were higher than normal and animals were less active. Although it appeared the over-winter survival was lower, what is more important is the probability of being observed and captured was greatly reduced. With so few animals at the surface in winter, sampling occasions for mark-recapture studies should be restricted to those times of the year when the majority of adult mussels are available at the surface. To arrive at better estimates and a better understanding of over-winter survival of freshwater mussels would require a large sampling effort with a considerable amount of excavation which may not be desirable.

Our models also indicated that apparent survival was size dependent. Adults had higher survival estimates than small animals, especially mussels over 55 mm in length (Fig. 1). *Elliptio complanata* >55 mm had a higher rate of survival (>91%) than smaller individuals, with an estimated survival rate of 69% for individuals 20 mm in length. We saw the same pattern for both *E. fisheriana* where animals >55 mm had >77% survival rate vs. 43% for animals 20 mm in length and *Lampsilis cariosa* where large mussels survived at a rate of >85% vs. 57% for small individuals. Survival rate approached 100% for all species for animals ≥ 100 mm in size. High survival estimates of adults compared to juveniles have been seen in other long-lived species where the annual survival rate is normally high (Brownie *et al.*, 1985). However, we suspect the apparent survival estimates, though lower than adults, may be higher for animals <55 mm in size than predicted by the models. Insufficient sample size of small animals resulted in the apparent survival rate estimates for these individuals having large variances.

TABLE 5.—Statistics for the candidate models for estimating movement of *Elliptio complanta*, *E. fisheriana* and *Lampsilis cariosa* between bands. The model likelihood is the ΔAIC_c weight for the model of interest divided by the ΔAIC_c weight of the best model. This value is the strength of evidence of this model relative to other models in the set of models considered. np is the number of parameters estimated

Model	ΔAIC_c	AIC Weight	Model Likelihood	np
S(t) $p(t)$ psi (bands constant, A&B differ, fix far upstream to 0)	0.00	0.89294	1.0000	21
S(t) $p(t)$ psi (bands constant, A to and from differ, fix far upstream to 0)	5.74	0.05058	0.0566	24
S(t) $p(t)$ psi (bands constant, B to and from differ, fix far upstream to 0)	6.36	0.03704	0.0415	25
S(t) $p(t)$ psi (fix far upstream to 0)	7.65	0.01944	0.0218	33
S(t) $p(t)$ psi (bands constant, fix far upstream to 0)	26.56	0.00000	0.0000	19

Most of the *E. complanata* (94%) were ≥ 55 mm, one *L. cariosa* was smaller than 55 mm and 60% of *E. fisheriana* that were tagged were ≥ 55 mm in length (Fig. 5). We accounted for some of the variation in survival and recapture by incorporating into the models our assumptions about these parameters, allowing survival and recapture to vary over time, by species or by size. Though our models indicated that time and animal size were important predictors of recapture probability, the assumption of equal catchability may have been violated despite no indication of any violation from the goodness of fit tests.

The assumption of equal catchability is violated when some individuals temporarily leave the sampling area (*i.e.*, in the case of mussels those that move below the surface and not available for detection in a given sampling period) and return during subsequent sampling occasions. This temporary emigration results in those animals below the surface temporarily having a zero capture probability while those available at the surface have a capture probability greater than zero. However, the buried mussels could return to the surface and be available for capture on the next sampling occasion and mussels that were available for capture the previous sampling occasion are now buried. There are two types of temporary emigration: completely random and Markovian (Kendall *et al.*, 1997). Temporary emigration is considered completely random when the probability that a mussel is buried is unrelated to whether it was buried in a previous sampling occasion. In Markovian temporary emigration whether a mussel is buried depends on its vertical position at the previous sampling occasion. We can realistically assume temporary emigration of adult mussels is a random event and therefore there would be little to no bias in the survival estimate (Carothers, 1973; Burnham, 1993; Hestbeck, 1995) though precision of the estimate may be reduced. We cannot assume completely random temporary emigration of small mussels since a small mussel buried at a previous sampling occasion is likely to remain buried until it reaches a larger size. Several studies have shown that small mussels remain buried beneath the substrate even during warmer periods of the year (Amyot and Downing, 1991; Balfour and Smock, 1995) when larger animals move to the surface. Balfour and Smock (1995) studied the vertical movement of *Elliptio complanata* and found that small animals remained below the surface until they reached about 50 mm in size. The large variances in the apparent survival estimates for small mussels and the low capture probabilities reflect a higher incidence of temporary emigration for this size group (Kendall *et al.*, 1997) than we had expected. The parameter values are, therefore, more difficult to interpret in

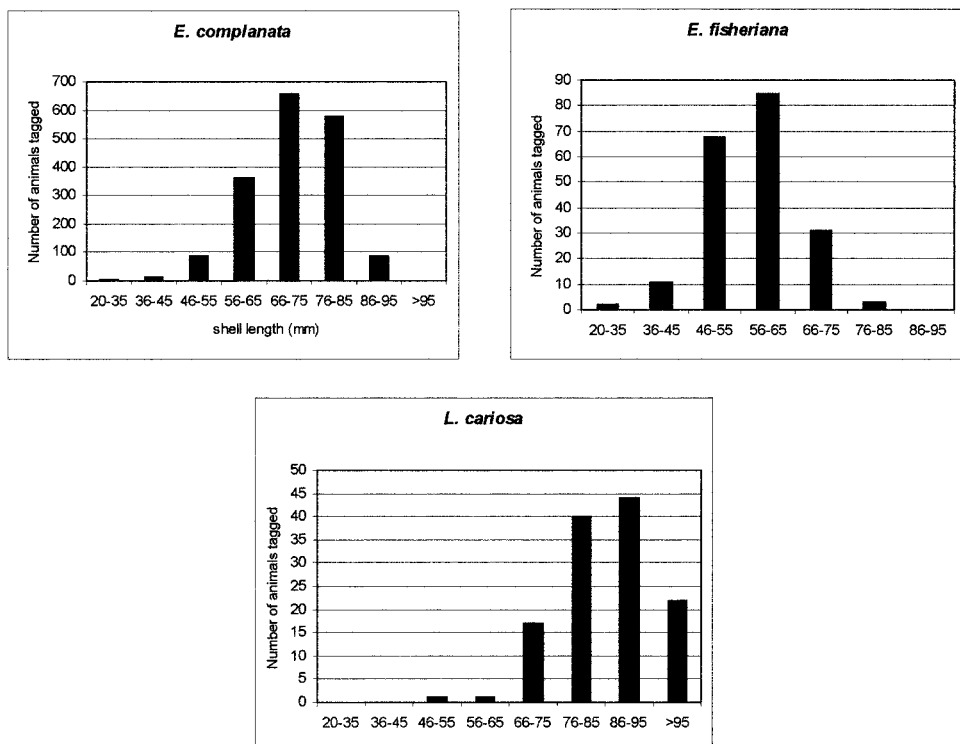


FIG. 5.—Size distribution of species based on total shell length measurements in mm

actual terms for this small size class which is more prone to emigration and more heterogeneous in their recapture rates. We concluded that temporary emigration was an important determinant of the seasonal pattern of recapture probabilities in this population. Unequal catchability is likely to exist in all capture-recapture studies to some degree due to imperfect detectability. Smith *et al.* (1999) found detectability of mussels varied by habitat and mussel size with differences in detection among substrate types greatest for smaller mussels. Though there is no study design to completely eliminate it, there are ways to reduce it. When it is suspected recapture probability may depend on some measurable characteristic such as sex or size that variable should be recorded so the sample can be stratified for analysis. In our case we had insufficient number of small animals to stratify our sample. Applying the robust design to estimate temporary emigration rate can be applied (Kendall *et al.*, 1997; Kendall and Bjorkland, 2001). The robust design involves sampling several times over a brief period (*e.g.*, sampling and tagging mussels each day for 3 d) to estimate capture probabilities using closed population models and then repeating this sampling annually so that vital rates can be estimated using open population models. This approach can be time consuming and often resources aren't available to implement this design. A preferred approach would be to include some amount of excavation to sample both buried mussels and mussels at the surface (Strayer and Smith 2003). The vertical position of individual mussels can be recorded on each sampling occasion. Multi-state models that allow for transition between locations (surface vs. buried)

could then be used to estimate survival of those at the surface and survival of those below the surface (Brownie *et al.*, 1993).

The high apparent survival estimates of adult mussels are similar to the survival estimates ($>97\%$) in a mark-recapture study of adult *Amblema plicata* (Say) (Hart *et al.*, 2001a) in Minnesota and the mean annual survival estimate ($94 \pm 3\%$) of adult *Elliptio dilatata* (Rafinesque) in Lake Pepin, Wisconsin, that were cleaned of zebra mussels (Hart *et al.*, 2001b). High survival (average survival $>97\%$) was also reported in a comparison of relocation studies involving multiple species of adult freshwater mussels after 2 y (Dunn *et al.*, 1999). Once these animals successfully pass the early vulnerable glochidia and juvenile life stages, the hard shell of the adult valves would provide some protection against adverse environmental conditions.

It is important to recognize the survival parameter (S) we were estimating is apparent survival which includes both mortality and permanent emigration. Therefore, estimates of apparent survival are almost certainly underestimates of true survival because some animals will also have emigrated from the study site. However, we believe there was little permanent emigration of animals at this site. Our model estimates indicated there was very little movement. Longitudinal movement of unionid mussels has been reported (Negus, 1966; Kat, 1982; Amyot and Downing, 1991, 1997; Balfour and Smock, 1995), but similar to our findings, most of this movement is infrequent (downstream movement rate of $<1\%$) and similar to the findings of Balfour and Smock (1995), mussels can move both upstream and downstream. While most of the downstream movement occurred within the 0 to 40 m distance, most of this movement probably was less than 40 m. Mussels moving over 10 m downstream have been documented in small streams (Kat, 1982; Balfour and Smock, 1995), but was shown to be rare. Some of this movement may be due to displacement by high flows, animals located near the top or bottom of one band and moving short distances into the adjoining band or misplacement of animals after tagging. While the rate of upstream movement was slightly greater than the rate of downstream movement (Fig. 4a), almost all of this movement occurred at the top of the site where there was very low current and substrate particle size was predominantly sand and silt. The upstream movement in the remaining bands was probably due to animals being located in close proximity to band boundaries. Mussels may move greater distances than previously thought and our results indicate that studies designed to monitor population trends or response of a mussel population to some perturbation need to ensure the size of the study site is large enough to detect movement. Continued tagging and capture occasions may help determine how far mussels move and by modeling movement rate with environmental and biological covariates such as sex, age or size, we may be able to determine why they move.

While several studies suggest considerable year to year variability in recruitment (Negus, 1966; Strayer *et al.*, 1981) both *Elliptio complanata* and *Lampsilis cariosa* had a low ($\leq 4\%$) and fairly constant rate of recruitment including an interval with no evident recruitment. Only *E. fisheriana* showed much variability in recruitment, which may reflect the variability in its habitat where changes in flow have greater effect on temperature, dissolved oxygen and area of available wetted habitat. Our models indicate that recruitment did occur for all species in 1996 through 1998 with virtually no annual recruitment for all three species for the interval of July 1999 to June 2000, suggesting that very few new animals were added to the population in June 2000 since the previous sampling in July 1999. Mean annual stream flow in 1999 and the first 6 mo of 2000 was approximately half the long-term mean stream flow for the same time period. Whether a year of no recruitment was an unusual occurrence that was due to adverse environmental conditions has yet to be determined. Additional capture occasions are needed to determine whether these species have occasional periods of

successful higher recruitment with longer intervals of low and possibly no recruitment or whether we happened to miss a large year class.

The recruitment parameter for open populations includes recruitment from both reproduction and immigration. Complicating our interpretation of these recruitment estimates for freshwater mussels is their need for a host to complete their life cycle. We cannot distinguish whether some of this recruitment was from reproduction in this population or was it from reproduction in another mussel bed upstream or downstream with new animals deposited by the fish host.

A second objective of this study was to evaluate how the survival and recruitment estimates influenced population trends over time. Though the structure of the top four models indicated both recruitment and rate of population growth vary over time the changes in growth between years was small. The average population growth rate (λ) approximated 1.0 for *Elliptio complanata* and *Lampsilis cariosa*, with both species experiencing slightly negative population growth between the fifth and sixth sampling interval. While the population was virtually static both within and between years for *E. complanata* and *L. cariosa*, average population growth over the same three year interval for *E. fisheriana* was slightly positive ($\lambda = 1.084$) with the intervals of higher positive growth corresponding to the intervals of highest recruitment. Whatever environmental cues trigger recruitment elicited basically the same response for all three species. Even though *E. fisheriana* had the lowest apparent survival rate for small individuals, the occasional intervals of higher recruitment and high annual adult survival enables the species to sustain some positive population growth. Sites with estimates of $\lambda \approx 1$ could reflect self-sustaining stationary populations, populations requiring high immigration to maintain stability or a combination of both. The λ estimates approximating 1.0 suggest the mussel population at this site on the Cacapon River supports a self-sustaining static population through a life history strategy of low, but constant recruitment and high annual adult survival to maintain stability. In variable environments, such as those inhabited by freshwater mussels, high adult survival rates probably allow individuals and populations to persist through potentially extended periods of less favorable reproductive conditions. Estimates of λ for this 4 y period should not be used to predict future population trends that can only be addressed by longer-term studies. However, with many native freshwater mussel populations experiencing declines, the trend in population growth rate does warrant some concern. Though low recruitment rates and low mortality of adults may be sufficient to maintain a population of these species at this location, it may not be sufficient to maintain a population at this site should a catastrophic event occur. The low recruitment rate of adults emphasizes the importance of ensuring the continued longevity of adult mussels and the importance of determining whether there are limiting factors to increasing recruitment in this population. While our models suggest recruitment may potentially be what is limiting population growth we do not know the factor or factors limiting recruitment.

Adult survival in long-lived vertebrate species is the sensitive demographic parameter affecting population change, whereas species with shorter life spans, fecundity is often more important in affecting change in the population (Boyce, 1992). High adult survival is a life history characteristic that is common to large mammals and vertebrates in general but is not found among other freshwater invertebrates. Unionids are unique among freshwater invertebrates both in their longevity and their high and constant adult survival. This life history strategy is instead similar to large mammals and some freshwater vertebrates such as hellbenders and some fish species. Their life history strategy can be considered a hybrid between an r and K-strategist. Unionids share some qualities of K-strategists (longevity and high adult survival) and they also share some of the qualities of r-strategists (high output of glochidia, lower survival of young, no parental care). It is possible that continuous (though

low) reproduction during a long adult life span can be beneficial for unionids and may be an evolutionary strategy in response to uncertain larval and juvenile survival. The survival estimates from this and other similar studies are an important contribution to the comparative data on freshwater mussels for several reasons. First, few estimates are available for freshwater species with such potential longevity. With environmental conditions varying between sites we would expect different rates of adult survival among populations, even those in close proximity. Therefore, a one size fits all management strategy may not ensure protection of a mussel population. To ensure the management plan will be effective it is important to develop estimates of survival and recruitment for additional populations. This may be difficult to achieve for some endangered species that are present in such low numbers making recapture probabilities too low to arrive at precise estimates of survival. Substituting information from other species or populations may not be appropriate unless the range of variability in survival and recruitment are known (Beissinger and Westphal, 1998). To arrive at better estimates of the variance in rates of survival, recruitment and movement requires measurements of these rates be made over a sufficient number of years to sample the range of environmental conditions. Secondly, the high survival rates of adult mussels in this and other populations suggests individuals may reach advanced ages not previously thought attainable in freshwater mussels inhabiting lotic systems. A mark-recapture study of freshwater mussels in lacustrine environments revealed high annual adult survival with mean age estimates for *Elliptio complanata* as high as 75 ± 29 y and 73 ± 50 y for *Lampsilis siliquoidea* (Barnes) (Anthony *et al.*, 2001). These estimates are not unlike some marine mollusks such as the hard clam, *Mercenaria mercenaria* (Linnaeus) which can live longer than 40 y (Eversole *et al.*, 2000) and the ocean quahog *Arctica islandica* (Linnaeus) which can live 100 y or more (Thompson *et al.*, 1980).

Pollock *et al.* (1990) and Burnham *et al.* (1987) have sections on the design of mark-recapture experiments. We offer a few guidelines for designing mark-recapture studies for freshwater mussel populations: (1) make sufficient effort to sample the entire study area so the sample population is representative of your target population and to ensure capture probabilities are high; (2) use either the robust design or include a sufficient level of excavation to address the issue of temporary emigration of mussels, especially for small size classes; (3) sample at a time of year when most mussels are likely to be available at the surface for capture; (4) use a tagging/marking method, such as double tagging, that does not influence survival rate and has a high tag retention rate to prevent losing information that can negatively bias the survival estimates; (5) tagged mussels should be returned to the areas where they were collected; and (6) mark and release a large number of animals on each sampling occasion. Brownie *et al.* (1985) recommend marking a minimum of 300 animals per year and more for animals that are expected to have low recapture rates. In our study we marked and released from 299 to over 500 animals during the summer sampling occasions. Finally, mark-recapture studies of freshwater mussels should be long-term. For long-lived species studies >10 y would be recommended as a minimum goal. Long-term mark-recapture studies can also be used to address the questions about senescence in freshwater mussels, which might be indicated by a decline in the survival probabilities with increasing age, with a model in which survival varied as a function of relative age of adults since they were first marked. Though exact age of individuals would not be known, one could test for a decline in survival with successive recaptures (and therefore aging) of individuals.

To date we have sampled and tagged on eight separate occasions over 4 y, a relatively short time frame for the study of a long-lived fauna. However, this study has provided some important insights into the ecology of freshwater mussels with additional tagging and capture occasions improving the precision of these population estimates. The study results

illustrate that tagging can be used to obtain estimates of important life history parameters of freshwater mussels and make inferences about the ecological relationships affecting population dynamics from the capture history of uniquely marked individuals. Additional replicated, long-term tagging studies are needed to place these findings into a broader ecological perspective. Long-term mark-recapture data sets can be an important source of information to test hypotheses about factors affecting not only survival but also recruitment, movement patterns and other aspects of population dynamics.

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